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THE NERVOUS SYSTEM OF CREPIDULA ADUNCA AND ITS DEVELOPMENT.

BY HAROLD HEATH.

The genus *Crepidula* in the vicinity of Monterey Bay, California, is abundantly represented by the members of two species, *C. adunca* and *C. nivea*. In each case the young are retained in capsules within the mantle cavity of the parent, and are liberated when they have attained the form of the adult and are in possession of all the definitive organs with the exception of those belonging to the reproductive system. It is accordingly readily possible to secure extensive series of embryos and to follow the course of development from the ovum to the adult. The embryology of several species of this genus has been studied in great detail by Conklin ('97),[1] and as a result it is clearly established that they all pursue essentially the same developmental path until they reach the veliger stage or a corresponding point where a free-swimming larva is lacking. Beyond this point nothing is known.

In connection with a comparative study of the nervous system of several families of mollusks, I have examined adults of the two above-mentioned species of *Crepidula* with considerable care and have traced its development in *C. adunca*. In view of the fact that *Paludina vivipara* as worked out by Erlanger ('92)[2] is the only other gastropod whose development in this respect is known, the results possess an enhanced degree of interest.

The central nervous system of the adult *C. adunca* is located in the base of the neck, in a spongy mass of connective tissue, placed between the pedal musculature and the overlying mantle cavity. It conforms to the highly centralized type characteristic of the monotocardia generally, with cerebral, pleural and pedal ganglia closely appressed. In several instances, especially in half-grown individuals, the line of demarcation between the cerebral and pleural ganglia is comparatively slight; on the other hand, the pedal ganglia are invariably sharply defined. All are globular bodies of essentially the same size and, as indicated previously, are united by comparatively short commissures and connectives.

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[1] The Embryology of Crepidula, *Journ. Morph.*, Vol. 13, 1897.

[2] Zur Entwicklung von *Paludina vivipara, Morph. Jahrb.*, Vol. 17, 1892.

Of the more peripheral portions of the nervous system the buccal ganglia are situated in the head region slightly attached to the dorsal face of the radular musculature. From the commissure uniting them two delicate nerves are given off, which course ventrally but rapidly become lost to view among the surrounding muscle bundles. The connectives to the cerebral ganglia arise from the forward borders of each buccal ganglion, extend laterally and anteriorly over the buccal musculature for a short distance, whereupon they pass between some of the bundles of radular muscles to the ventral side of the head. In this position, at each side of the under surface of the radula, they pursue a course posteriorly to the cerebral ganglia. Immediately after reaching the ventral surface of the head they are united by a delicate commissure.

Each cerebral ganglion gives rise anteriorly to one or two nerves, in addition to the buccal connective, which innervate the head. Where one nerve appears it soon divides into an outer and inner branch destined to supply the tentacle and lips, respectively. The relatively strong tentacle nerve gives off a short, stout nerve to the eye and, after dividing, extends far towards the tip of the tentacle. The inner, or lip nerve, passes by a fairly direct path to the dorsal side of the head, and ultimately breaks up in the tissue about the mouth.

The pedal ganglia usually develop four pairs of nerves. The most anterior, springing from the forward border of the ganglion, extends through the pedal musculature to the forward section of the foot, where each branches repeatedly and becomes lost among the muscle fibres. Two other pairs extend ventrally and likewise soon disappear in the compact pedal musculature. In addition to these three pairs, each pedal ganglion gives off from its antero-dorsal surface another nerve destined to supply the base of the neck. On the left side of the body the bundle is comparatively slender and soon becomes lost to view at the junction of the head and mantle. On the right side the corresponding branch has the same size and apparent distribution in lately hatched individuals, but at a later period it becomes greatly enlarged and supplies the penis, which arises relatively late in life. It may be added that the pedal ganglia are united by two commissures, the usual heavy one and another, much more delicate, posterior to it.

The elements of the visceral loop comprise three clearly defined ganglia, the sub-intestinal, the supra-intestinal and the visceral. The first named is a globular body of approximately the same size as the overlying right pleural ganglion, to which it is attached by a short connective, thus producing a dextral zygoneury, while a somewhat larger connective, passing ventral to the pharynx, unites it with the left pleural ganglion. The supra-intestinal ganglion is a fusiform mass united by a short connective to the right pleural. The visceral ganglion, in contact with the ventral floor of the mantle cavity on the right side of the body, is joined by connectives passing

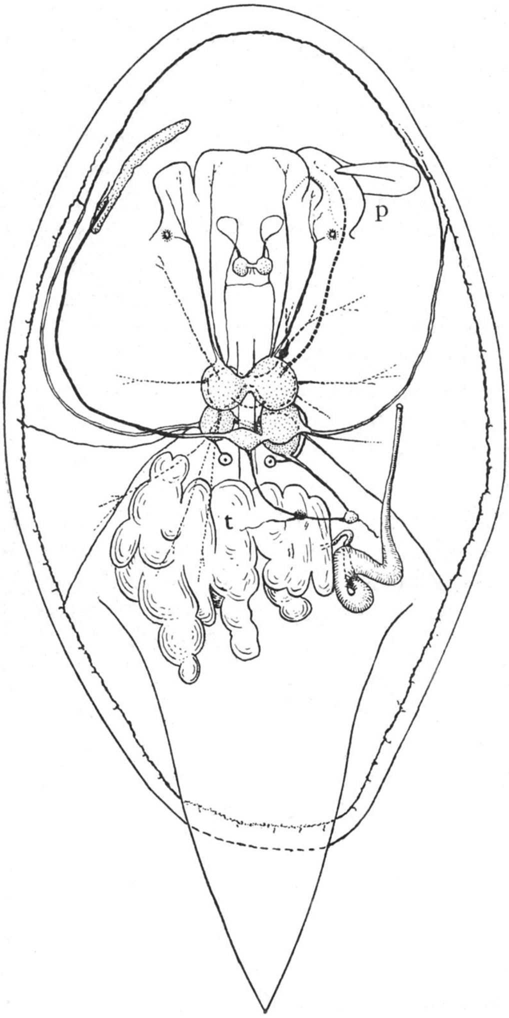

Fig. 1.—Dorsal view of the nervous system of *Crepidula adunca*. The pedal nerves are represented by broken lines; the right posterior pedal nerve is omitted. p., penis; t., testis.

dorsal to the œsophagus and to the right side of the stomach and the adjacent section of the intestine. The visceral connective on the left develops a small nerve, usually associated with a ganglionic enlargement, which has been traced for a short distance beneath the floor of the mantle cavity. The visceral ganglion itself also gives rise to a branch which passes to the wall of the kidney, where it disappears from view.

In this species a well-defined marginal mantle nerve, or *Mantelrandnerv*, is present with many of the essential features of what has been found by Willcox ('98)[3] to exist in *Acmæa fragilis*. In the present instance it is loosely attached to the walls of the marginal mantle sinus, and throughout its course develops numerous delicate branches, which attach to the overlying epithelium or the deeper-seated gland cells. On the right side of the body this marginal nerve is united by two connectives with the pleural ganglion, and, judging from sections, with the sub-intestinal ganglion as well. Of these connectives the anterior is much the heavier, and skirting the floor of the mantle cavity can be followed forward, where it divides into a short, lateral branch uniting with the marginal nerve coming up from the posterior three-fourths of the body, and a slightly more dorsal and relatively larger nerve coursing about the base of the marginal mantle thickening. In other words, the marginal mantle nerve of the posterior part of the body can be traced as far forward as the anterior level of the head in contracted specimens. It actually may continue entirely around the body, but anteriorly it becomes very delicate and finally disappears among the masses of gland cells in the free border of the mantle. However, the heavy connective from the right pleural ganglion attaches to it before its disappearance, and on the other hand extends around the mantle edge in front, where it meets the corresponding nerve from the left pleural ganglion, thus completing the circular mantle nerve, though, as noted before, this anterior section is at a slightly greater distance from the mantle border. The smaller, posterior connective appears to be more largely a product of the sub-intestinal ganglion, and, like the two smaller connectives of the left side, it extends laterally and posteriorly through the pedal musculature to the mantle border. These two smaller connectives of the left side as well as another of much larger caliber arise from the pleural ganglion. The anterior one pursues a course similar to its counterpart on the right and is inserted in practically the same fashion with the marginal mantle nerve.

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[3] Zur Anatomie von Acmæa fragilis, *Jenaische Zeitschr. f. Naturw.*, Bd. 32, 1898.

The osphradial ganglion is a well-defined elongated body situated far forward on the left side of the mantle cavity. The nerve leaving its posterior border pursues a parallel course with the anterior mantle ring connective and enters the supra-intestinal ganglion. Certain species of the genus *Crepidula* are reported.[4] to possess a sinistral zygoneury wherein the supra-intestinal ganglion is united to the pleural of the same side. I have found no evidence of its existence in *C. adunca*.

Turning now to the development of the nervous system, we find that shortly after the first appearance of the foot the ectodermal cells immediately in front of the lateral angles of the mouth opening commence to elongate, and each area rapidly differentiates into a well-defined, probably sensory ridge and the tentacle. Associated with these external developments there is a migration of ectodermal cells from the region of the ridge and tentacle, slight at first, but rapidly increasing, and finally ending, if one can rely on sections, at the time when pigment first makes its appearance in the eye. These migrant cells form the cerebral ganglia, more or less rounded at first, and largely obscured by the heavily staining overlying ectoderm.

Synchronous with the development of the cerebral ganglia the pedal ganglia arise. With the exception of a median, ciliated, slender, wedge-like area, the base facing anteriorly, the cells of the foot likewise become elongated, whereupon cells migrate inwards, forming two large, diffuse masses in contact posteriorly where the commissure subsequently arises. The four ganglionic bodies thus existing at this time appear to be the product solely of migrating elements, since sections give no indication of cell division after the cells have left the ectodermal layer. The same is also true of all the other ganglia now to be considered.

In whole mounts and in sections the cells along the posterior border of each cerebral ganglion can be seen in the late stages of its development to assume an elongated form and to develop fibres which extend posteriorly. In some instances the strands thus produced form two distinct bundles at the outset, one of which passes into the pedal ganglion, while the other at a slightly later stage joins with the pleural. In other instances one bundle first appears and subsequently divides to form the cerebro-pedal and cerebro-pleural connectives. During this time the cells of the anterior margin of each cerebral ganglion likewise elongate and rapidly form fibres which extend across the midline and thus form the cerebral commissure.

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[4] Lang's Lehrbuch, p. 213.

The buccal are the only ganglia which do not directly arise from cells migrating from the overlying ectoderm; on the other hand, they give clear evidence of being products of the cerebral ganglia. At about the same time that the cerebral commissure is forming cells can be seen extending toward the midline from the inner border of each cerebral ganglion. These gradually form an accumulation on each side of the radular invagination, and in some instances completely invest the radular sac. In the stage represented by fig. 2 the ganglia are usually differentiated, though the commissure and

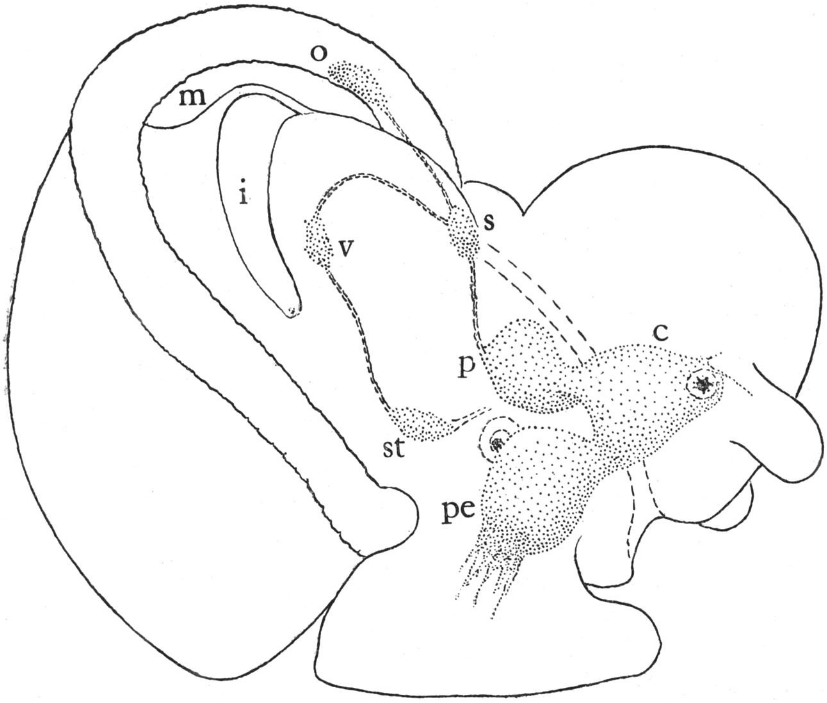

Fig. 2.—Half-developed embryo of *Crepidula adunca*, showing the central nervous system and the visceral loop. c., cerebral ganglion and eye; i., intestine; m., mantle cavity; o., osphradial ganglion; p., pleural ganglion; pe., pedal ganglion and otocyst; s., supra-intestinal ganglion; st., sub-intestinal ganglion; v., visceral ganglion.

the connectives may continue to contain cells until a relatively late stage in the development of the embryo.

After the cerebral ganglia have developed, yet before they have become fashioned into their final form, the pleural ganglia and the elements of the visceral loop put in their final appearance. Each pleural ganglion is the product of cells migrating from the adjacent ectoderm and arises at the sides of the body immediately posterior and slightly dorsal to the cerebral ganglion. In most instances it is a fairly sharply defined though sheet-like structure, yet it may originate in the form of several distinct masses whose anastomosing fibres form a distinct plexus before they become fused into a single mass.

The ganglia of the visceral loop arise simultaneously. The sub-intestinal occupies a position on the right side of the body at the intersection of the neck and visceral mass; the supra-intestinal lies approximately in the midline at the junction of the neck and visceral mass; while the visceral ganglion is somewhat to the right of the midline and anterior to the terminal section of the intestine. Even while these ganglia are in process of formation delicate fibrils from some of the component, bipolar cells push out between the yolk granules and increasing in number ultimately form the connectives of the visceral loop. The osphradial ganglion rapidly becomes imbedded in the margin of the mantle, and, as in the adult, is united by a connective with the supra-intestinal ganglion. In many instances a delicate connective unites the sub- and supra-intestinal ganglia; no trace of it has been found to exist in adult specimens. The right-sided zygoneurous condition, the union of the pleural and the sub-intestinal ganglion, characteristic of the adult appears to put in an appearance shortly before the embryo escapes from the parent.

At the time of hatching there are traces of a plexus extending about the margin of the mantle, but it is very dim and indistinct. When it becomes clearly defined throughout and capable of being traced it has all of the essential features of the marginal mantle nerve of the adult.

With the increased growth of the mantle and the development of an extensive mantle cavity (beyond the stage represented in text fig. 2) the visceral mass between the mantle margin and the neck becomes completely covered. Furthermore, the absorption of the included yolk creates a more flattened condition of the embryo, which ultimately brings the nervous system into the position characteristic of the adult.